Know thine enemy

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Female-female aggression can promote stable color polymorphism

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Abstract

The co-existence of ecologically similar species has been a longstanding problem in evolutionary ecology. Theory and experimental work suggest that co-existence is promoted if territorial males bias aggression towards phenotypically similar rivals, generating negative frequency-dependent selection between species. We propose that where females are territorial, the same mechanism in females may promote species co-existence too. We studied a haplochromine cichlid species from Lake Victoria, *Neochromis omnicaeruleus*, in which three distinct female color morphs co-exist. In the laboratory we tested for aggression biases in wild-caught females of each morph with stimulus females of every morph, enclosed in transparent tubes. Females of each morph biased aggression towards stimulus females of their own morph, suggesting that females of all three morphs may have an advantage when their morph is locally the least abundant. This mechanism may contribute to stabilizing the color polymorphism. The absence of aggression bias in blotched and plain sisters bred by crossing a blotched and a plain parent suggest that genetic linkage cannot explain the observed association between color and aggression bias in nature despite hybridization between morphs. We discuss alternative hypotheses that could explain the association. We conclude that female-female aggression may be an important force for stabilizing speciation and species co-existence.

Introduction

The colorful haplochromine cichlid species flocks of the Great African Lakes are the most extreme examples of explosive speciation among vertebrates. Most of the astounding species diversity in Lake Victoria likely evolved from a few ancestors in the past 15.000 years (Johnson et al. 1996; 2000; Seehausen 2006a). A great diversity of trophic adaptations has evolved rapidly, associated with strong habitat and trophic resource partitioning among the major lineages (Seehausen 1996; Seehausen et al. 1999a). However, many immediate sister species co-exist in sympatry with apparently little, if any ecological differentiation but with marked differences in male nuptial coloration (Bouton et al. 1997; Seehausen et al. 1999a,b). The same pattern repeats itself in the older radiation of haplochromines in Lake Malawi (Seehausen et al. 1999a; Danley & Kocher 2001; Kocher 2004; Genner & Turner 2005). The sympatric co-existence of ecologically similar species that differ mainly just in nuptial coloration (or color morphs in the case of ongoing gene-flow) is a longstanding problem in ecology (in haplochromines: e.g. Reinthal 1990; Seehausen 1996; Bouton et al. 1997; Genner et al 1999a; 1999b; Genner & Turner 2005; other: e.g. Hutchinson 1961; Scheffer & Van Nes 2006). One idea is that negative frequency-dependent selection on male nuptial coloration may arise from male-male aggression, thereby promoting species co-existence (Mikami et al. 2004; Seehausen & Schluter 2004; this thesis). Haplochromine males vigorously defend long-term mating territories to secure spawnings (Parker & Kornfield 1996; Maan et al. 2004). Competition over territories is intense, and is likely to influence male fitness. Negative frequency-dependent selection on color could arise if territorial males direct more aggression to phenotypically similar than to dissimilar rivals. Such an aggression bias would lead to rare phenotypes sustaining less intense competition, and thereby enjoying a fitness advantage relative to the more abundant phenotype. Experimental evidence confirms that males of some haplochromine cichlids species preferentially direct aggression towards males of their own species (chapter 2 & 3). Comparative evidence suggests that such interaction may structure haplochromine species composition in nature (Seehausen & Schluter 2004).

In haplochromine cichlids female-female competition is likely to affect female fitness as well. Haplochromines are female mouth brooders and maternal fry guarders. Females aggressively fend off small territories to protect their fry. In algae-scraping species, such as *Neochromis omnicaeruleus,* females often occupy short term territories over rocky sites to secure access to algae (Seehausen 1996). Finally, territories can also provide shelter against piscine and avian predators. Therefore, interference competition among females for territories is likely, and could exert selection on female coloration too. Females of most haplochromine cichlid species are cryptically colored, consistent with their larger role in parental care (Fryer & Iles 1972; Seehausen 1996). Due to this crypsis, females of closely related species often look phenotypically similar, providing less opportunity for

color-based recognition of competitors and aggression biasing. However, conspicuous female color phenotypes are common in several haplochromine species (Lande et al. 2001), including the highly polymorphic species *Neochromis omnicaeruleus* (Seehausen et al. 1999b). In its Makobe island population, three distinct color morphs occur in both sexes: a plain presumably ancestral morph (P), and two conspicuously colored blotched forms, white blotched (WB; black blotches on white) and orange blotched (OB; black blotches on orange). The WB and OB morph is predominantly found in females. Intermediates between these morphs exist but are rare. A long term series of field data from 1991 to 2003 suggests morph frequencies have fluctuated little over at least 12 years (Seehausen et al. 1999b; Maan 2006). Females are quite aggressive and territorial too (Seehausen et al. 1999b; Maan 2006). The existence of intermediate phenotypes suggests there is gene-flow between morphs (Seehausen et al. 1999b), and their microhabitat distribution is completely overlapping (Seehausen & Bouton 1997), raising the question how this color polymorphism is maintained (Seehausen et al. 1999b; Lande et al. 2001).

We tested in wild-caught females of *Neochromis omnicaeruleus* whether territory defenders bias aggression towards competitors of their own color morph, using a simulated intruder choice test (chapter 2, 3 & 5). We show that females of each color morph differ in aggression bias in the predicted direction: females of each morph exhibit an own-morph bias in aggression, which may generate negative frequency-dependence on female coloration. This then raises the question how the association between color and aggression bias is maintained in the face of gene-flow. Gene-flow would quickly erode any associations between color and aggression bias genes by assortment and recombination. We tested whether genetic linkage (via pleiotropy or physical linkage) between color and aggression bias could maintain the own-morph bias in aggression. We examined aggression biases of plain and blotched sisters bred from a plain and a blotched parent. Genetic linkage, but not independent inheritance, predicts own-morph aggression biases in both plain and blotched sisters to be retained, and hence a difference in aggression bias between the two morphs.

Methods

Species

We studied a population of *Neochromis omnicaeruleus* from Makobe Island in the western Speke Gulf (Tanzania) that consists of three fully sympatric morphs. Biogeographical data, field observations and laboratory experiments suggest that plain (P) is the ancestral morph, and orange blotched (OB) and white blotched (WB) are two derived morphs or incipient species at Makobe Island (Seehausen et al. 1999b). P females are yellow to brown with 4-8 dark vertical bars, whereas most P males are blue and some are yellow. OB individuals have variably shaped brown

blotches, superimposed on an orange or pink background. WB individuals have variably shaped black blotches on a white to brassy background. Even though half of the females in the population are blotched, only less than 1.7% of the males are blotched. The three morphs are fully sympatric and ecologically indistinguishable, but partially reproductively isolated by male and female mating preferences. Males (and not females) of the blotched morph exhibit mating preferences against the P morph, and males and females of the P morph exhibit strong mating preferences against the blotched morphs (Seehausen et al. 1999b). Nevertheless, intermediate phenotypes occur, suggesting gene flow.

Subjects and housing

Females were collected in Lake Victoria around Makobe Island, and transported to the laboratory in Haren, The Netherlands, in February 2003. We tested 15 OB, 16 P and 15 WB morph females, all wild-caught. We generated plain and blotched full sib sisters by crossing a blotched with a P parent (blotch is X-linked; Seehausen et al. 1999b). The laboratory crossings are summarized in table 1. With one exception, we used different wild-caught fish for each cross (table 1). We made two cross types: OB female with P male (OBxP), and WB female with P male (WBxP). We also made one cross between a P female and a WB male. All five OBxP families contained P (henceforth P_{ob}) and OB females, and P males (table 1). All five WBxP families contained P (henceforth P_{wb}) and WB females, and P males, consistent with an existing model of inheritance (Seehausen et al. 1999b). In one of the WBxP families and in the PxWB family we also had one WB male each (table 1).

Females grew up in sib-groups, guarded by their mother for the first four weeks post-hatching. We removed males as soon as the sexes differentiated around 6 months of age. When individuals began to mature at an age of 4-5 months, we added 10-15 juvenile *Pundamilia* sp. to each family to disperse aggression. *Pundamilia* are less aggressive than *Neochromis omnicaeruleus*, and are commonly used as dither fish in our breeding aquaria. We tested 18 OB, 13 P_{ob}, 22 WB and 16 P_{wb} lab-bred females. The number of females tested per sib-group is shown in table 1.

All aquarium walls, except the front, were covered with black plastic sheets. All aquaria were connected to a central biological filtration system and water circulated continuously. Water temperature was kept at 25 ± 2°C and a 12:12 h light:dark cycle was maintained. The bottom of the aquaria was covered with gravel. Fish were fed flake food (Tetra Min Tropical Fish Flakes) seven times per week.

Pre-experimentation housing

For at least one week prior to the experiments females were individually housed in separate compartments with a PVC tube as a refuge. Approximately ten compartments were made in 100-170 liter aquaria using transparent perspex sheets. Females had one or two direct neighbors, and visual access to all other females in

the tank. The arrangement ensured that females became territorial and avoided unwanted effects of social isolation, while preventing them to engage in physical interaction. Wild-caught females were visually exposed to females of all three morphs. Lab-bred females were visually exposed only to females of their own morph and that of their sisters. Test females were never housed adjacent to the corresponding stimulus females.

Table 1 Summary of the crosses to generate lab-bred plain and blotched females. Shown are the family code, morph of mother, father, the number of sons and daughters. Note that these numbers represent the moment when females were transferred from sib-groups to the pre-experimentation housing. Numbers at the moment of fry release were different due to mortality. Also shown are the number of plain and blotched daughters that we tested. All parents were wild-caught, unless indicated otherwise (F1=mother bred from wild-caught parents).

OBxP family code	Mother	Father	Sons		Daughters		Nr of daughters tested	
			P	OB	P	OB	P	OB
1	OB	P	4	0	3	12	3	4
2	OB (F1)	P	5	0	3	11	3	5
3	OB	P	6	0	1	4	1	3
4	OB	P	7	0	5	8	1	1
5	OB[1)]	P	?	0	11	13	5	4
						total:	13	17

WBxP family code	Mother	Father	Sons		Daughters		Nr of daughters tested	
			P	WB	P	WB	P	WB
1	WB	P	4	0	3	1	1	1
2	WB	P	3	0	16	14	6	5
3	WB	P	9	0	3	18	2	5
4	WB(F1)	P	2	0	5	8	2	2
5	WB[2)]	P	5	1	22	12	4	4
6	P	WB	8	1	4	27	1	4
						total:	16	21

[1)] This female bred twice with two different males: broods were raised together in a single aquarium

[2)] This is a combined brood of two females and a single male: broods were raised together in a single aquarium

Simulated intruder choice test

We used a simulated intruder choice test to estimate aggression biases. Test females were allowed to become territorial, and were then presented with stimulus females in paired combinations (WB-OB, P-OB and P-WB). Wild-caught test females were tested only with stimulus pair combinations that contained their own morph, thus each wild-caught female was presented with two stimulus pairs. These two stimulus pairs were selected from standard length matched stimulus trios (OB, P and WB). Lab-bred P_{ob} and OB were tested with P-OB stimulus pairs, and lab-bred P_{wb} and WB were tested with P-WB stimulus pairs. No stimulus pair was used more than once with either morph. A test aquarium consisted of a large experimental compartment (55 x 35 x 39 cm, l x w x h) for the test fish, and a smaller compartment (5 x 35 x 39 cm) for a dither neighbor, needed to maintain territorial condition of the test fish. The dither neighbor was a small female of an unrelated Lake Victoria cichlid (*Pundamilia nyererei* [Witte-Maas & Witte, 1985]). It was separated from the test fish by a transparent partition. Test females were transferred from the pre-experimentation housing aquarium to the experimental compartment one day before a trial to allow acclimatization to the test aquarium. A PVC tube was provided as a refuge.

At the start of a trial, two stimulus females, individually confined in transparent watertight Perspex tubes, were placed in the experimental compartment 20 cm apart from one another and at the end of the tank opposite to the neighbor fish. No chemical communication was possible between stimulus and test fish. The test females perceived the stimulus females as intruders, and typically responded aggressively to both stimulus females, whilst the neighboring *P. nyererei* female was entirely neglected. We recorded the number of attacks of the test female to each of the stimulus females for five minutes starting directly after introduction of the stimulus females. An attack was defined as biting or butting at the walls of the tube containing the stimulus female. An attack was terminated with a display event, or when the test female turned away from the stimulus female (chapter 3). Across trials we randomly assigned stimulus females to left and right positions. The sequence in which the two stimulus pair combinations were presented to wild-caught test females was randomized too. After a female had been tested, she was used as a stimulus female to test other females. The interval between testing a female, and using her as a stimulus was at least one day. Every female was tested before she was used as a stimulus.

Analysis

A female's *aggression level* was estimated by the total number of attacks she launched in 5 minutes averaged over all trials of that female. We tested for differences in the level of aggression between morphs using ANOVAs.

Aggression biases could be expressed in two ways. The *attack ratio towards females of a particular morph* was calculated as the number of attacks

launched against the stimulus females of that morph divided by the total number of attacks launched to both stimulus females in the same trial. A similar aggression bias was calculated as the *attack ratio towards females of the own morph*. We first tested whether females differed in attack ratio using independent t-tests. We then tested whether females had a significant aggression bias towards their own color morph, using a doubly nested repeated-measure ANOVA (RM-ANOVA), with 'morph of test female' (3 levels) as explanatory variable. The first repeat (referred to as 'stimulus pair') consisted of attack ratios towards own morph for the two stimulus female pairs with which a test female was tested. The second repeat (referred to as 'bias') was nested within the 'stimulus pair' repeat. It evaluated aggression biases by testing whether the attack ratio towards own morph deviated significantly from 50%. We also computed an RM-ANOVA for females of each morph separately. The results of the 'stimulus pair' repeat are not involved in any hypothesis testing, and is therefore not reported. Separate post-hoc tests to evaluate aggression biases for each morph and stimulus pair combination separately was done by testing the attack ratio against 50% using paired t-tests.

For the analysis of the lab-bred females, we first tested for each cross type (WBxP or OBxP) separately whether family explained any significant fraction of the variance in the attack ratio. To this end, we used linear hierarchical models (Bryk & Raudenbush 1993) in MlWin 2.0, using a two level model with individual fish nested within families. The response variable was the attack ratio towards P morph, and the explanatory variable was 'morph of test female'. Family explain none of the variance in attack ratio in any of the cross types (family in both cross types: $Ps>0.5$). We therefore treated each female as an independent data point in subsequent data analysis. We tested for genetic linkage between color and aggression bias against the alternative of independent inheritance of both traits by comparing the attack ratio of plain and blotched females towards P using independent t-tests. A difference in aggression bias would support genetic linkage.

One wild-caught WB female and one lab-bred WB and OB female launched no attacks at all and were not included in the analysis of aggression bias. To meet assumptions of parametric testing, we arcsine square root transformed the attack ratio data, and square root transformed the aggression level data. All reported probabilities are for two-tailed tests. Statistical analyses were performed in SPSS 12.0.1 unless stated otherwise.

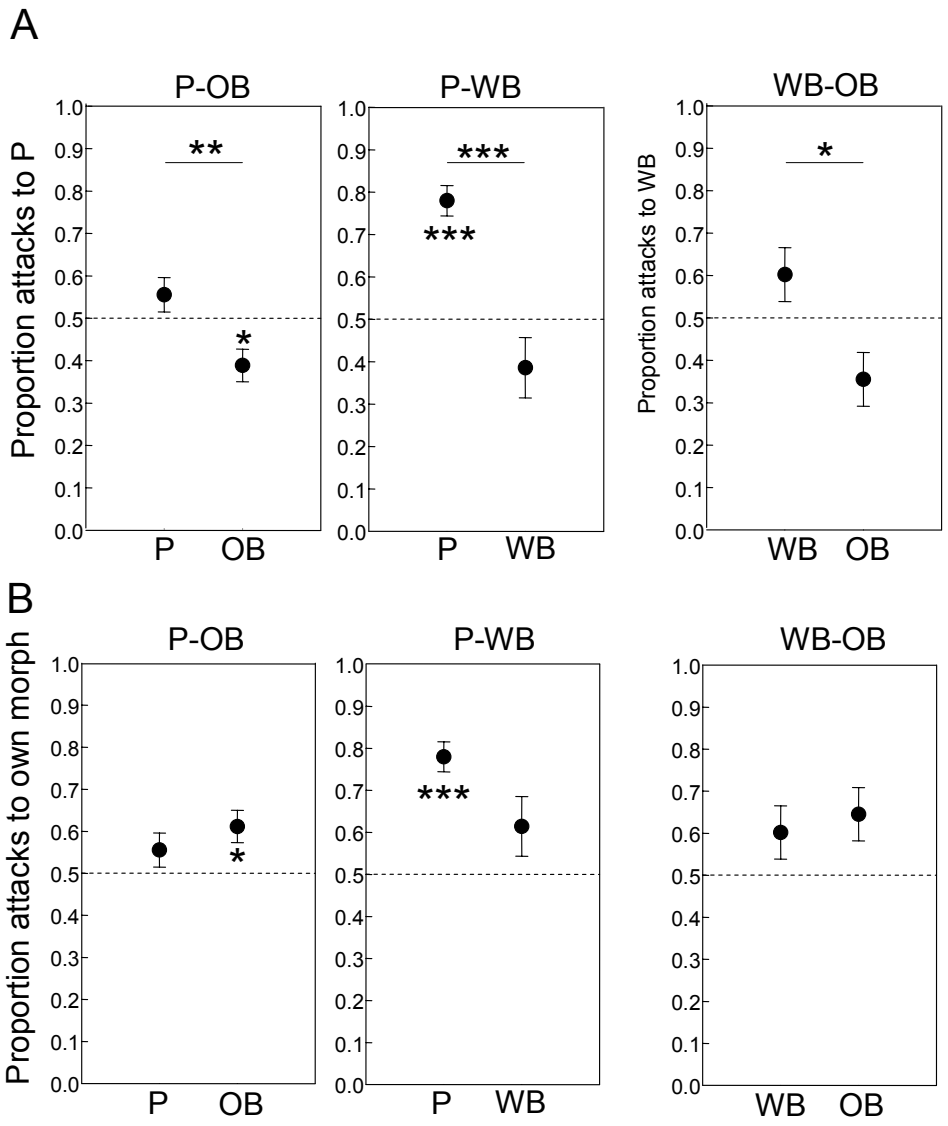

Figure 1A The attack ratio (mean ± SE) of wild-caught females of each color morph (indicated at the bottom) for each stimulus pair combination (indicated on top). The attack ratio is expressed as the proportion of attacks towards one morph (P in the P-OB and P-WB combination, and WB in the WB-OB combination) relative to the total number of attacks. An attack ratio of 0.5 represents identical numbers of attacks to both stimuli (------). Indicated are differences in attack ratio between females of different morphs and significant deviations from 50% (for statistics see text). (*P<0.05, **P<0.01, ***P<0.001).

Figure 1B Same as 1A, but here the attack ratio is expressed as the proportion attacks to one morph.

Aggression bias in wild-caught females

The aggression level of OB females was 43.9 ± 5.7 attacks/5 min (mean ± standard errors), that of P females was 47.3 ± 5.7, and that of WB females 38.7 ± 4.7. These differences were not statistically significant (ANOVA $F_{2,43}$=0.65, P=0.53).

The mean aggression biases towards a particular morph of wild-caught females are shown in figure 1A. Females of different color morphs differed in aggression biases. This was revealed by testing within each stimulus pair combination the bias of females of both morphs as expressed as attack ratio towards females of the same morph (Figure 1B, table 2). Thus, P and OB differed significantly in aggression bias when tested with a P-OB stimulus pair (independent t-test: t_{29}=-2.84, P<0.01), P and WB females too differed when tested with a P-WB stimulus pair (t_{30}=-4.23, P<0.001), and finally, WB and OB females differed when tested with a WB-OB stimulus pair (t_{29}=2.28, P<0.05). All differences were in the direction predicted by own-morph aggression bias.

The mean aggression biases towards own morph of wild-caught females are presented in figure 1B for each stimulus pair combination. Overall, females preferentially attacked their own morph ('bias' repeat [against 50%], $F_{1, 42}$=23.24, P<0.001). The magnitude of this own-morph bias was not different between morphs (Figure 1, morph of test female, $F_{2,42}$=0.68, P=0.51).

Repeating the same nested RM-ANOVA for females of each morph separately detected significant own-morph biases in aggression in P and OB females, but not in WB females (OB: $F_{1,14}$=7.4, P=0.02, P: $F_{1,15}$=64.1, P=<0.001, WB: $F_{1,13}$=2.1, P=0.17). Further post-hoc tests consisted of testing for each morph and stimulus pair combination separately if the attack ratio deviated from 50% (table 2). Significant own-morph biases were retained for OB females when presented with an OB-P stimulus pair, and for P females when presented with a P-WB stimulus pair (see figure 1B).

Aggression bias in lab-bred females: genetic linkage?

The aggression level of P_{ob} females was 32.6 ± 6.3 attacks/5min (mean ± standard errors), that of OB females 33.2 ± 6.1, of P_{wb} females 34.6 ± 6.0 and of WB females 27.3 ± 4.3. There was no difference in aggression levels between females from OBxP families and females from WBxP families (ANOVA, cross type [OBxP versus WBxP]: $F_{1, 65}$=0.084, P=0.77), nor between blotched and plain individuals (ANOVA, color morph [blotched versus plain]: $F_{1, 65}$=0.639, P=0.43). Neither did the interaction term between both factors contribute significantly to the explained variance (cross type x color morph: $F_{1,65}$=0.341, P=0.56).

The mean attack ratio towards P is shown in figure 2A, and towards own morph in figure 2B. Genetic linkage between color and aggression bias predicts a difference in aggression bias between blotched and plain females. Neither P_{ob} and OB (independent t-test: t_{28}=1.38, P=0.18), nor P_{wb} and WB (t_{35}=-0.293, P=0.77)

differed in the attack ratio towards P (Figure 2A, table 2). The results make genetic linkage unlikely explanations for the own-morph aggression biases observed in wild-caught females.

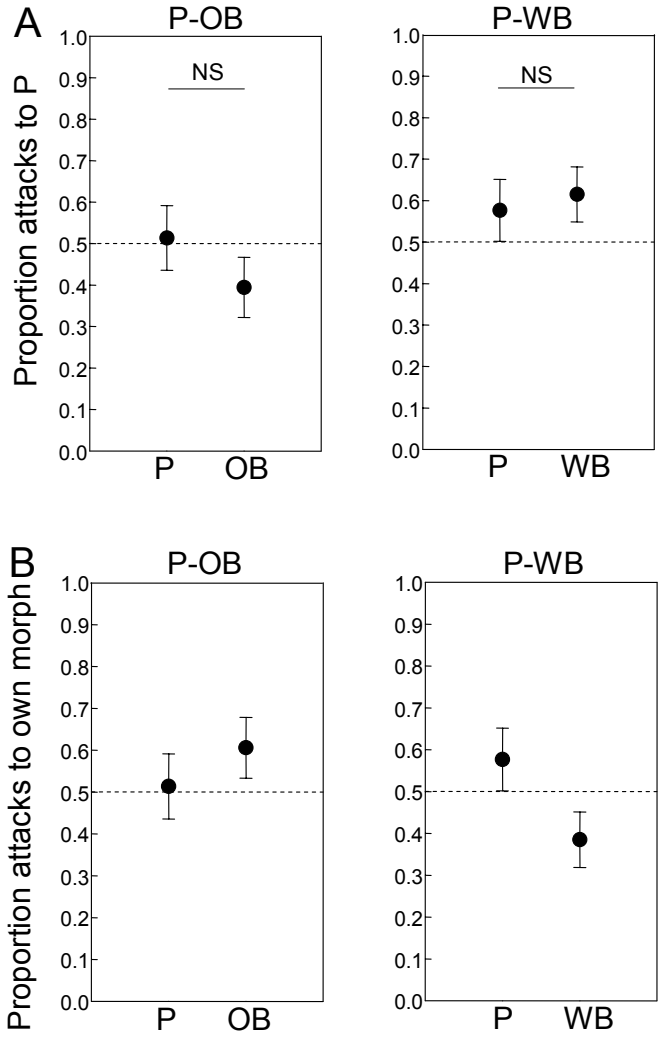

Figure 2A The attack ratio (mean ± SE) for lab-bred OB and P_{ob} females derived from OBxP families (left panel), and for lab-bred WB and P_{wb} females derived from WBxP families (right panel). The attack ratio is expressed as the proportion of attacks to P relative to the total number of attacks. An attack ratio of 0.5 represents identical number of attacks to both stimuli (------). Deviation from 50% is tested using paired t-tests. None of these was significant. There was no differences in attack ratio between morphs (NS=nonsignificant, for statistics see text).

Figure 2B Same as 2A, but here the attack ratio is expressed as the proportion attacks to own morph.

We tested for females of each morph separately whether lab-bred females preferentially attacked females of their own morph by testing whether the attack ratio deviated from 50% (Figure 2A, table 2). None of the female groups showed any preference to attack own morph, whereas WB females showed a nonsignificant tendency to preferentially attack P females.

Table 2 The aggression bias expressed as the attack ratio towards one morph for wild-caught and lab-bred females, calculated as the number of attacks to one morph divided by the total number of attacks (equivalent to figure 1B and 2B, see also note). Indicated are means ± SE. To assess aggression bias, the attack ratio is tested against 50% using paired t-tests. Shown are the t statistic and the P value. Significant effects are indicated in bold.

morph		stimulus pair combination	attack ratio[1)]		test against 50% (paired t-test)	
wild-caught	N		mean	SE	t	P
P	16	P-OB	0.56	0.04	1.26	0.23
OB	15	P-OB	0.39	0.04	-2.75	0.02
P	16	P-WB	0.78	0.04	-5.97	<0.001
WB	14	P-WB	0.39	0.08	-1.30	0.21
WB	14	WB-OB	0.60	0.06	-1.49	0.16
OB	15	WB-OB	0.36	0.06	1.74	0.10
lab-bred						
P_{ob}	13	P-OB	0.52	0.08	0.34	0.74
OB	17	P-OB	0.40	0.07	-1.64	0.12
P_{wb}	16	P-WB	0.58	0.07	1.34	0.20
WB	21	P-WB	0.61	0.07	1.96	0.06

[1)] Attack ratio expressed as proportion of attacks to P (in the P-OB stimulus pair), to WB (in the WB-OB) and to P (in the P-OB)

Discussion

Using a simulated intruder choice test and wild-caught fish, we found aggression biases towards own morph among female color morphs of *Neochromis omnicaeruleus*. These results suggest that in competition for territories, females of all three morphs may receive fewer attacks, and thereby experience elevated fitness when their morph is locally the least abundant of the three. Elevated fitness may

come about via a higher probability to gain access to limiting food resources, or shelter from predators. Shelter is important both for females themselves and for their fry. The negative frequency-dependent selection that is expected to arise from this own-morph aggression bias may both facilitate the invasion of a novel color type, and stabilize a color polymorphism once it is there (Mikami et al. 2004; Seehausen & Schluter 2004).

Why do females of *Neochromis omnicaeruleus* bias aggression towards self-colored females, even though all three morphs compete for the same ecological resources (Seehausen & Bouton 1997; Seehausen et al. 1999b)? We can only speculate about this question. Perhaps the answer lies in mutual mate choice and female competition for mates. In *Neochromis omnicaeruleus*, males (and not females) of the blotched morph exhibit mating preferences against the P morph. Females and most males of the P morph exhibit strong mating preferences against the blotched morphs (Seehausen et al. 1999b; Pierotti & Seehausen 2006). Mutual mate choice would render females of the same morph competing more strongly for males with the same preference (see also Lande et al. 2001). Therefore, females would benefit from directing more aggression to rival females of their own morph with whom they share the same potential partners. The choosiness of males suggests that such mate competition among females exists.

The *Neochromis omnicaeruleus* system has inspired models of sympatric speciation by sexual selection (Lande et al. 2001; Kocher 2004, see also Seehausen et al. 1999b: Pierotti & Seehausen 2006). The selective mating among colour morphs led Seehausen et al (1999b) to suggest that the *Neochromis omnicaeruleus* system has properties of an incipient stage of sympatric speciation by sexual selection. Forces that can account for polymorphism in female mating preferences are essential to the process of sympatric speciation by sexual selection (Van Doorn et al. 2004). In this context it is interesting to note that recent theory indicated the importance of female-female competition in generating and maintaining such a polymorphism (Van Doorn et al. 2004). Own-morph aggression biases among females could contribute to the evolution of a female-preference polymorphism by creating negative frequency-dependent selection on female preference.

Given the evidence for gene-flow among the *Neochromis omnicaeruleus* morphs (Seehausen et al. 1999b) the question how the association between color and aggression bias is maintained is intriguing. In theory, if own-morph biases in aggression are expressed pleiotropically with color, the emergence and co-existence of incipient species would be greatly facilitated. Such linkage or pleiotropy between color and preference genes, even though perhaps unlikely at first sight, has recently been demonstrated in *Heliconius* butterflies (Kronforst et al. 2006). We tested for genetic linkage by examining aggression biases of lab-bred plain and blotched sisters from morph crosses, but neither found any difference in aggression bias between plain and blotched females, nor any own-morph bias. Thus, genetic linkage (through pleiotropy or physical linkage) is unlikely to explain the observed own-morph biases in aggression of wild-caught females. The results make the

alternative, independent inheritance of colour and aggression bias more likely. The absence of evidence of genetic linkage suggest that the association between color and aggression bias observed in wild-caught females has to be maintained either by a high degree of assortative mating among morphs, or by strong selection against recombinant phenotypes or both. This is consistent with the hypothesis of Seehausen and co-workers (1999b) that morphs are partially isolated by male and female mating preferences. However, the incompleteness of behavioral isolation and the breakdown of the association between color and aggression bias in the first hybrid generation, leaves questions open as to the level of gene-flow between morphs and the strength of selection against color-behavior recombinants.

In conclusion, our study shows that wild-caught females of *Neochromis omnicaeruleus* bias aggression towards females of their own color morph. Such an aggression bias was originally proposed for competition among males resulting in negative frequency-dependent selection on male colour (Mikami et al. 2004; Seehausen & Schluter 2004; Van Doorn et al. 2004; chapter 2-7). The reproductive output of haplochromine populations is likely limited by survival and energy intake of females, and not much by that of males (Genner et al. 1999b). Territorial interactions between females are thus likely to be important for recruitment of competing color morphs or species, affecting their potential to co-exist. Blotch color polymorphisms are common in cichlids in several African Lakes (Lande et al. 2001; Kocher 2004). It would be interesting to see how common female aggression biases are in these systems.

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